Periodicity of Aradus cinnamomeus (Heteroptera, Aradidae) in northern Europe

KARI HELIÖVAARA & RAUNO VÄISÄNEN

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General characteristics of the life-cycle rhythms of *Aradus cinnamomeus* are described in Scandinavia and compared to previous studies from Finland. The species normally has a two-year life-cycle in most parts of its range, but at higher latitudes and altitudes the life-cycle takes three years. In the Åland archipelago and possibly on Gotland the life-cycle takes three years. Reproduction takes place in even years in most parts of the two-year area, while in western Finland and in western Sweden there are wide areas where the bugs reproduce almost exclusively in odd years.

Normally one of the alternate-year cohorts almost exclusively predominates, the shifts in preponderance being relatively sharp. The three-year cohorts usually coexist in subequal numbers in quite an irregular fashion. It is suggested that one of the alternate-year cohorts prevents the increase in density of the other generation by inducing defensive chemical changes in the pine. In the area of three-year life-cycle the *Aradus*-induced chemical changes are suggested to decrease due to the harsh climatic conditons, thus permitting the coexistence of allochronic bug cohorts.

K. Heliövaara, Finnish Forest Research Institute, Pl 18, SF-01301 Vantaa, Finland.
R. Väisänen, Zoological Museum, University of Helsinki, P. Rautatiek. 13, SF-00100 Helsinki, Finland.

Introduction

The pine bark bug *Aradus cinnamomeus* (Panzer) is a periodical species with more or less distinct reproductively isolated allochronic populations or cohorts. These cohorts are either sympatric or parapatric, depending on the life-cycle rhythm concerned and the geographical scale used in the analysis. Examples of similar periodical phenomena among insects are numerous (Bulmer 1977): the alternate–year flight of certain Lepidoptera (e.g. Valle 1933, Suomalainen 1937, Mikkola 1976, Imby & Palmqvist 1978, Douwes 1981), the periodical appearance of the North American 13 and 17-year cicadas (Lloyd & Dybas 1966a, b, Simon et al. 1981, Lloyd et al. 1983), and the European cockchafers (Hurpin 1962, Niklas 1974). These species show unusual biogeographical patterns which are not only exciting curiosities of nature, but of wider interest to ecologists and entomologists.

Documentation of the pattern is a prerequisity for further discussion on the alternative hypotheses proposed to explain these phenomena. Here, we describe the general characteristics of the distribution and life-cycle rhythms of *Aradus cinnamomeus* in Scandinavia, as compared to previous investigations from Finland (Heliövaara & Väisänen 1984a, b, 1986, 1987, Heliövaara et al., in press). This areal extension of the study provides further evidence for determining which of the various explanations of the pattern is most feasible. The pine bark bug was studied in Sweden by Brammanis (1975) especially, whose biogeographical findings are discussed and re-evaluated.

The pine bark bug is a hemimetabolous sapsucker living on young Scots pines (*Pinus sylvestris*) and preferring dry sunny forests and pine bogs. It has caused serious damage on pine stands in many parts of Eurasia, including esker ridges of southern Finland. The life-cycle of the bug normally takes two years. The bugs overwinter first as fourth instar nymphs and, after maturation in Au-

gust–September of their second summer, again as adults. The adults mate and reproduce normally during the following spring. In the north the life-cycle is prolonged to three years (Brammanis 1975).

Material and methods

Only scattered records of the life-cycle of the pine bark bug in Scandinavia are available (Brammanis 1975, Heliövaara & Väisänen 1987). In the present study new data were gathered from various parts of the area, mainly during two longer excursions in July 1986 and August 1987. Altogether about 60 sample localities were examined. A questionnaire was also sent to forest zoologists, and a few well-known specialists were consulted.

The bug samples were collected from pine saplings growing along roadsides. Bark was removed from several pine trunks until at least 10 bugs had been found. The developmental stage of the bugs was determined on every plot.

Results

The distribution of the pine bark bugs with different life-cycle rhythms in northern Europe is mapped in Fig. 1. The picture that emerges from this investigation in Scandinavia is very similar to that of the Finnish one. In the southern and central parts of the study area the life-cycle of the bug takes two years, while in the north the bugs have a three-year development. Generally, the even-year cohort almost exclusively dominates where the bugs are biennial, i.e. in eastern and central Finland, eastern and central Sweden, and south-eastern Norway. However, in large areas in both western Finland and western Sweden, as well as in some areas in Norway, the odd-year bugs almost exclusively predominate. There appears to be only a narrow transition zone between the allochronic cohorts in Sweden, as in Finland where the pattern is especially sharp (parapatry). In southern Sweden and Norway the pine bark bug appears to be less abundant than in southern Finland. This is probably simply due to the lack of suitable habitats, dry sandy heath forest and pine bogs with pine saplings. In Estonia, the even-year cohort apparently predominates (20 even-year bugs from Poltraaga, 1 odd-year bug from Tartu).

In northern Fennoscandia the life-cycle of the bug takes three years. However, the three-year area extends much further to the south on the Swedish than on the Finnish Bothnian coast, although the exact location of the transition zone between a two and three-year development period was not clarified. There are difficulties in interpreting the samples collected near Sundsvall in central Sweden and at Hamar in southern Norway. They may represent normal three-year bugs, or two-year bugs reproducing in the odd years, or a mixture of these two groups. In Finland there is a narrow belt of odd-year bugs between even and three-year bugs in the area N of Jyväskylä, while in the area E of Kokkola this seems to be missing. The transition zone between the two and three-year bugs seems in any case to be wider and more complex than that between even and odd-year bugs. In the Scandinavian mountains and at many localities in central Norway, the bug seems to be rare or absent in spite of the availability of suitable young pines.

In Sweden, the area between Kristianstad and Karlskrona is somewhat enigmatic in our own material. It may either represent a transition zone between the even and odd-year bugs or a narrow coastal area of three-year bugs. The samples contained adults and nymphs of more than one instar. This may be partially due to the collecting time since individual differences are usually conspicuous but decrease towards the autumn. Furthermore, the unusually cold and rainy summer in 1987 makes interpretation difficult in certain cases (two-year bugs: unusually small nymphs due to the weather conditions; or three-year bugs: normal cohort of young nymphs). Also the situation in Denmark deserves further studies.

Discussion

The results on the periodicity of the pine bark bug agree with previous investigations from Finland (Heliövaara & Väisänen 1987) and, in fact, the most interesting result may be that the Scandinavian pattern is so conspicuously similar to that in Finland. Brammanis (1975) had already observed that in Sweden the odd-year bugs predominate in Dalekarlien (Siljanfors) and in southern Halland (Laholm, Tylösand, Falkenberg). The odd-year area now appeared to be extensive in southwestern Sweden. The predominance of odd-year bugs in both western Finland and western Sweden would appear fascinating. What could explain such similar blocks of "wrong"-year bugs? Our in-

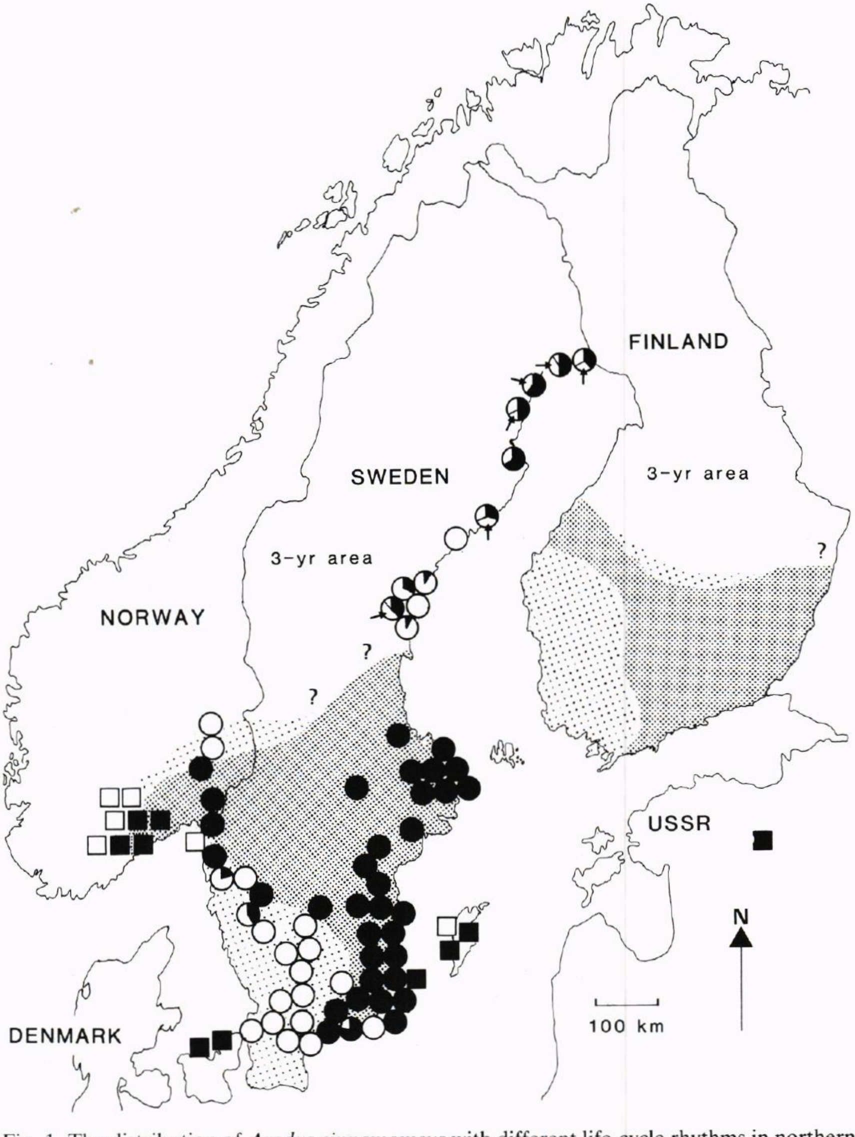

Fig. 1. The distribution of *Aradus cinnamomeus* with different life-cycle rhythms in northern Europe. Dark grey—even-year area, light grey—odd-year area. The proportions of the cohorts in August 1987 are given in the sample pies as follows: black—adults, white—small larvae (instars I–III), white with arrows—medium-sized larvae (instar IV). Additional museum samples examined and data based on literature references are indicated by squares coloured respectively. All samples from southernmost Sweden have been interpreted to represent two-year bugs. The Finnish distribution is based on Heliövaara & Väisänen (1987), the records from Gotland on Brammanis (1975) and from southeastern Norway partially on Pettersen (1975).

Livscykelrytmer hos *Aradus cinnamomeus* i olika delar av Nordeuropa. Två-årig livscykel finns både med vuxna under jämna (mörkgrått) resp udda (ljusgrått) år. I ringar och kvadrater anges proportionerna av vuxna (svart), små nymfer (vitt), resp medelstora nymfer (vitt med pil) för augusti 1987. Ringarna baseras på egna insamlingar, medan kvadraterna redovisar proportioner beräknade utifrån litteraturuppgifter resp djur i museisamlingar. Alla prov från sydligaste Sverige har ansetts representera två-åriga stinkflyn.

terpretation is, however, quite trivial. We believe that the similarity is primarily due to chance. The odd-year bug blocks lying in the middle of areas predominated by even-year bugs may have been caused by a weather catastrophe (cf. Valle 1933) that has destroyed the original preponderance relationships by decreasing the population densities to such a low level that the odd-year bugs can conquer "empty areas".

Dispersal could provide another explanation. In the areas where the three-year life-cycle is predominant, all the three cohorts usually coexist in subequal numbers. A three-year area close to a two-year area could function as a "random dominance generator" and change the two-year cycle from an even to an odd year one. This is possible in Finland if the bugs have penetrated via the Åland archipelago or northern areas, while in Scandinavia this may have taken place via the northern areas, the mountains or possibly southern Sweden (if three-year bugs exist there). Elsewhere in Europe, the even-year bugs are said to predominate, but small odd-year cohorts have been observed in the Kiev region (Tropin 1949) and in Czechoslovakia (Turček 1964). In Poland the pine bark bug has been reported to reproduce mainly in odd years (Strawinski 1925).

As mentioned above, the life-cycle of the bug takes three years in the Åland archipelago in Finland (Heliövaara & Väisänen 1987). Samples examined from Öland clearly represent the even-year cohort observed by Brammanis (1975). However, he found that the bugs commonly reproduced in all years in Mästermyr on Gotland, while at other sites on the island (Klintehamn, Roma) the bugs reproduced mainly in even years. These confusing records from Gotland may, in fact, suggest that the bug also has a three-year life-cycle on Gotland, at least occasionally. It is also possible that even and odd-year cohorts predominate locally, and that samples from Mästermyr were from a transition zone.

The predominance of even and odd-year bugs in different areas, in a parapatric pattern, requires an explanation. The reason why the odd-year cohort cannot invade successfully the area where even-year bugs abound (and vice versa), seems to be due to the relationships between the cohorts themselves. One cohort appears to prevent the dispersal and increase in density of the other one. We have suggested that the mechanism might be intraspecific interference competition, reinforced by the impact of parasitoids (Heliövaara & Väisänen 1984b). The interference may be mediated chemically by the pine.

It has been reported that the polyphenol content of *Pinus sylvestris* changes after attack by *Neodiprion sertifer* (Thielges 1968). Mechanical damage to *Pinus ponderosa* can cause changes in phenols, procyanins and protein in the foliage (Wagner & Evans 1985). Recently, Leather et al. (1987) reported that insect-induced chemical changes caused by previous defoliation in young *Pinus contorta* have a negative effect on the oviposition, growth and survival of *Panolis flammea*. Furthermore, adult females were able to distinguish between host plants with and without previous defoliation, and lay their eggs so as to take advantage of these differences. We thus suggest that the *Aradus* female can distinguish between pines which have and which have not been attacked by another *Aradus* cohort. Studies on the chemical changes caused by *Aradus* attack in pines are in progress. We have observed in field experiments that the presence of one cohort has a negative effect on the other one, suggesting heavy intraspecific competition that may be pine mediated (Heliövaara & Väisänen 1986). Studies do not support the idea that predators or diseases would have a central role in maintaining the status quo in the present biogeographical pattern (Heliövaara & Väisänen 1984b, Hokkanen et al. 1987).

Another important question concerns the fact that three cohorts of *Aradus* usually coexist in the three-year life-cycle area, while in the two-year area one of the cohorts almost exclusively predominates. If the parasitoids were the key factor controlling the pattern, then the limit between two and three-year areas would be the limit of the range of the parasitoid species. If intraspecific competition was the key factor, the pattern could be explained by adopting the stress hypothesis (White 1984). In the north pines may grow under such severe climatic conditions that their chemical defence mechanisms against insect herbivores have deteriorated, and the intraspecific competition mediated by the pine would thus be small. Furthermore, in the three competitive cohort system the rate of disappearance of a smaller cohort or cohorts may be substantially lower than that in the system consisting of two competitive cohorts, although the intensity of competition would be the same (Heliövaara & Väisänen 1987).

Some evidence supporting the latter pine-

mediated competition hypothesis was obtained from a study on *Retinia resinella* (L.) (Lepidoptera, Tortricidae) in northern Europe (Heliövaara & Väisänen, manuscript). In both these species the limit between the two and three-year life-cycle areas runs almost in the same way (except in the Åland archipelago). According to the parasitoid hypothesis, we must assume that both the specific parasitoids of *Aradus* and the specific parasitoids of *Retinia* (these species have no common parasitoids) would have the same distribution limits in the north. In the case of the pine-mediated competition hypothesis we only have to assume that the stress caused by climate breaks down the chemical defence mechanisms of the pine. Thus the same assumption could be adopted for both *Aradus* and *Retinia*.

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Sammanfattning

Tallbarkstinkflyet, *Aradus cinnamomeus*, har normalt en två-årig livscykel, men i norra Skandinavien och norra Finland är den tre-årig. Där livscykeln är tre-årig så överlappar de tre generationerna helt och vuxna djur förekommer varje år. Så är inte fallet där livscykeln är två-årig, och vuxna djur förekommer här endast vartannat år. Denna periodicitet hos tallbarkstinkflyet är märklig såtillvida att regionalt förekommer de vuxna och reproducerar sig antingen på udda eller jämna år. Både i Sverige och Finland så förekommer vuxna djur på udda år i den sydvästra delen, samt i ett smalt bälte längs gränsen mot det tre-åriga området. Att generationerna är åtskilda när livscykeln är två-årig kan förklaras av att den ena kohorten hindrar den andras tillväxt genom att stimulera tallens kemiska försvar. I mer nordliga områden, där livscykeln är treårig, är tallens kemiska försvar ej lika effektivt, och de tre generationerna kan samexistera.

Recension

Vögtle, F. & Schuss, W. 1985. *Spiegelstereoskop.* VCH Verlagsgesellschaft, Weinheim, Västtyskland. Pris: 48:- DM (Bestell-Nr. 1010097).

Insekterna är genom sin stora färgprakt och formrikedom mycket lämpade för fotografisk avbildning. Emellertid blir resultatet inte alltid det önskvärda, t ex kan bilden sakna djup eller djurets kroppsform kanske inte framträder riktigt. Vad man då skulle behöva är någon slags tredimensionell bild av objektet. En sådan kan fås genom att två fotografiska avbildningar av samma objekt, tagna ur något olika vinklar, betraktas bredvid varandra i ett s k stereoskop.

Stereobilder är vanliga inom kemin där de på ett enkelt sätt kan åskådliggöra komplicerade strukturer. Flertalet av de äldre stereoskopen kräver dock speciella bildformat och avstånd mellan bildparen. Det av Vögtle och Schuss konstruerade spegelstereoskopet gör det möjligt att betrakta bilder av alla format, från små papperskopior till stora projicerade diabilder. Till spegelstereoskopet medföljer tre olika exempel på stereobilder samt en kort handledning. Principen är enkel, vid fotograferingen flyttas kameran i sidled 1/30 av avståndet mellan motiv och film. Resultatet blir förvånansvärt bra, t ex vid avbildning av stora tjocka vandrande pinnar i lövverk, vårtbeklädda paddor, däggdjurskranier, blommor m m. Beroende på kamerautrustning och fantasi kan det mesta avbildas för att betraktas tredimensionellt: detaljer av insekter, enskilda insekter, insekter i parning, grupper av insekter, biotoper eller landskap av speciellt intresse för olika arter.

För den som fotograferar insekter (och naturligtvis andra djur och växter) är detta spegelstereoskop ett ypperligt hjälpmedel för ett elegant åskådliggörande av motiven. Även inom undervisning och forskning på våra högskolor torde tillämpningar finnas.

Ulf Carlberg